# A Taxonomic Review of the Genus Spathius Nees (Hymenoptera: Braconidae) In North America and Comments on the Biological Control of the Emerald Ash Borer (Coleoptera: Buprestidae)

Paul M. Marsh and John S. Strazanac\*

(PMM) Collaborating Scientist, Systematic Entomology Laboratory, USDA, Washington, DC, mailing address: P.O. Box 384, North Newton, KS 67117, USA; email: swampy@wildblue.net

(JSS) Plant and Soil Sciences/Entomology, West Virginia University, Morgantown, WV 26506, USA; email: jstrazan@wvu.edu

Abstract.—A review of the braconid genus Spathius in North America and comments on several species in the biological control of the Emerald ash borer, Agrilus planipennis Fair., are presented. Separate keys to females and males, descriptions, distributions, and biologies are given for the 19 species occurring in North America. One new species, Spathius leiopleuron Marsh and Strazanac, n. sp., is described and six new synonymies are proposed as follows: S. floridanus Ashmead (=S. simillimus Ashmead, n. syn.); S. laflammei Provancher (=S. benefactor Matthews, n. syn.); S. rubidus (Rossi) (=S. aphenges Matthews, n. syn.); S. sequoiae Ashmead (=S. canadensis Ashmead, n. syn., S. tomoci Ashmead, n. syn., and S. claripennis Ashmead, n. syn.).

In 2002 a new exotic forest pest, Agrilus planipennis Fairmaire (Coleoptera: Buprestidae), the emerald ash borer (EAB), was discovered in Michigan and Ontario (Haack et al. 2002; Herms et al. 2004). This pest is native to northeastern China, Korea, Mongolia, Japan, Taiwan, and the Russian Far East. In China, the only recorded hosts are several species of ash (Oleacea: Fraxinus) but it has been recorded from species of Pterocarya (Juglandaceae) and Ulmus (Ulmaceae) in other parts of its native range. In North America, EAB has spread from Michigan and Ontario to Indiana, Missouri, Ohio, Wisconsin, Pennsylvania, West Virginia, Virginia, and Maryland (nursery stock) and has been found to attack all native species of ash.

Shortly after the discovery of EAB in North America, an aggressive control program was established by the USDA Forest Service, Michigan State University, and the Chinese Academy of Forestry. This

included programs to search for natural enemies of EAB both in China and North America. During explorations in China, a species of the braconid wasp genus Spathius Nees was discovered which attacked EAB larvae, and preliminary biology and field studies were conducted. This species has subsequently been described as Spathius agrili Yang (Yang et al. 2005) and its biology and biocontrol potential are presently being studied in Michigan and China. At the same time, explorations for native natural enemies attacking EAB in North America were started. A number of species of parasitoids were reared in association with EAB, with the Braconidae sent to one of us (PMM) for identification (Bauer et al. 2005). Among the species associated with EAB were specimens of two species of the braconid genus Spathius: numerous specimens of S. floridanus Ashmead, which occurs throughout eastern North America and has been recorded from several species of Agrilus Curtis; and one female and three males of an unde-

<sup>\*</sup> Author for correspondence

scribed species of *Spathius* (see discussion of this species at end of paper).

The discovery of S. agrili in China with its potential for biocontrol of EAB and the subsequent rearing of S. floridanus in association with EAB in North America provided an opportunity to study the genus Spathius in North America. Matthews (1970) presented a revision of the genus Spathius for North America. In this study, we present a revision of Matthew's monograph, including a revised key to species, updated descriptions, synonymies, SEM illustrations of all species, updated distributions and host ranges, and notes on species that might have potential as further parasitoids of EAB. During the course of this study, one new species was discovered, and six new synonyms are proposed.

#### MATERIALS AND METHODS

Several thousand specimens of *Spathius* were borrowed for study from the following institutions: National Museum of Natural History, Washington, DC; American Entomological Institute, Gainesville, FL; Texas A&M University, College Station, TX; California Academy of Sciences, San Francisco, CA; Canadian National Collection, Ottawa, Canada. In addition, specimens were received from biocontrol workers at Michigan State University, and from the USDA Systematic Entomology Laboratory.

Specimens were examined using a Wild M5 stereomicroscope. Scanning electron micrographs were made using the Hitachi S-3500N scanning electron microscope at the Department of Entomology, Kansas State University. Wing photographs were made using a Nikon D100 digital camera mounted on a Leica MZ16 at West Virginia University. The SEM images and wing photographs were enhanced and plates composed using Photoshop (Adobe Systems Incorporated, San Jose, CA) by JSS.

Sculpturing on the body is important in determining species in *Spathius*. Most of the terminology used follows that proposed by Harris (1979). However, some

variations were proposed by Marsh (2002) in his study of the Doryctinae of Costa Rica and the reader is referred to both of these works for definitions of the sculpturing and wing venation terminology. The term precoxal sulcus is used for sternaulus, as proposed by Wharton (2006).

#### Genus Spathius Nees

Spathius Nees 1818:301.

Stenophasmus Smith 1859:169. Synonymized by Szépligeti 1904.

Euspathius Foerster 1862:236. Emendation of Spathius.

Pseudospathius Szépligeti 1902:58. Synonymized by Belokobyl'skij 1992.

Rhacospathius Cameron 1905:86. Synonymized by Wilkinson 1931.

Diagnosis.—Head cubical, temples broad, occipital carina present and complete; first flagellomere equal to or longer than second; notauli distinct; precoxal sulcus distinct and variously sculptured; metasoma petiolate, first segment narrow at base, more or less parallel sided and suddenly widened at apex, length often several times greater than width; ovipositor at least as long as metasoma beyond petiole, often much longer than entire body; fore tibia with single or double row of 15-50 stout spines along anterior edge; hind coxa with antero-ventral tooth at base; fore wing vein r-m present, vein m-cu meeting vein 2M beyond vein 2RS, first subdiscal cell closed at apex, vein 3CU leaving cell well above middle and often on same line as vein 1CU.

Distribution.—Cosmopolitan; especially common in the Old World tropics; rare in Central and South America with one recorded species; 19 species occur in North America.

Comments.—In North America, this genus is easily distinguished from all other genera of the subfamily Doryctinae by the petiolate metasoma, and the venation of the fore wing with vein m-cu meeting vein 2M beyond vein 2RS and the closed first subdiscal cell. The subfamily Doryctinae

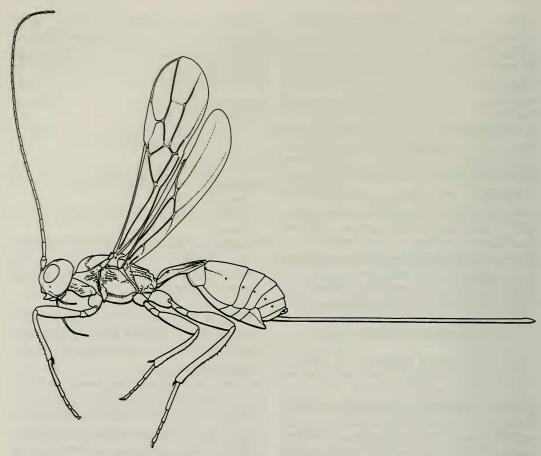


Figure 1. Spathius habitus. (Wharton et al. 1997, used with permission.)

and the genus *Spathius* can be identified using keys provided in Wharton et al. (1997) and Marsh (1997), respectively. In 1973, Matthews and Marsh established the genus *Notiospathius* for the Neotropical species previously included in the genus *Spathius*. Although recent phylogenetic studies (Zaldivar-Riverón et al. 2007, 2008) have shown that the two genera are not closely related, they are similar morphologically and can be distinguished using the keys provided by Marsh (1997, 2002).

Nixon (1943) presented a revision of the Old World *Spathius* in which he separated the species into nearly 50 species groups. Matthews (1970) stated "Although in a few cases the Nearctic species could be construed to fit certain of Nixon's (1943) groups of Old World *Spathius...*, none possess the

exact combination of characteristics of these groups;...". We agree with this statement. Although many of the North American species seem to agree with Nixon's exarator-group, most cannot be placed accurately in any of these groups. Matthews did separate the species into what he called natural groupings and gave them group names. However, we have also found these groupings to be difficult to define and, thus, have not used species-groups in this study.

Separate keys to females and males are provided below. Males are always more difficult to identify because usually they are smaller and the characters less distinct. The key to males may be difficult to use and the best way to distinguish males is by association with females in rearings or by DNA analysis.

#### KEY TO THE NORTH AMERICAN SPECIES OF SPATHIUS NEES

#### Females

1.	Precoxal sulcus with distinct carina along lower margin extending from epicnemial carina to mid-coxal cavity (Figs 4B, 19B)
	Precoxal sulcus without a distinct carina along lower margin
2(1).	Fore wing vein 2RS longer than vein 3RSa (Fig 19F); ovipositor longer than
-(1).	metasoma trifasciatus Riley
	Fore wing vein 2RS equal in length, or nearly so, to vein 3RSa (Fig 4H); ovipositor
_	shorter than metasoma
2(1)	Eyes small, malar space at least 3/4 eye height, often equal (Figs 2A, 13A, 18A) 4
3(1).	
4(2)	Eyes larger, malar space at most 1/2 eye height
4(3).	Ovipositor at least twice as long as metasoma
- -	Ovipositor at most as long as metasoma
5(4).	Scutellum rugose (Fig 13D); vertex and temple smooth (Figs 13A, B) marshi Matthews
- ((5)	Scutellum smooth (Fig 2D); vertex and temples rugulose (Figs. 2A, B)
6(5).	Maxillary palpus very short, at most equal to eye height brevipalpus Matthews
- F(0)	Maxillary palpus longer, usually twice eye height brachyurus Ashmead
7(3).	Petiole long and narrow, at least as long as 1.5 times length of middle femur, usually
	longer, in side view gently sloping toward base (Figs 5D–E, 7D, 8D–E) 8
-	Petiole shorter, never longer than 1.5 length of middle femur, in side view strongly
0 (=)	arched at base (Fig 16D)
8(7).	Scutellum smooth and polished (only male known) longipetiolatus Ashmead
_	Scutellum not smooth, usually weakly acinose or acinose
9(8).	Metasomal terga 2-4 distinctly and completely sculptured (Fig 5F), lateral margin of
	terga 2+3 sharp and distinct its entire length; fore wing vein 3CU interstitial and on
	same line as vein 1CU (Fig 5G)
-	Metasomal terga 3 and 4 smooth, lateral margin of terga 2+3 sharp only at base; fore
	wing vein 3CU not on same line as vein 1CU, thus vein 2CU present (Figs 7F, 8G) 10
10(9).	Vertex transversely striate, at least directly behind ocelli (Fig 8A); metasomal terga 2–3
	completely sculptured on basal 3/4; hind tarsomere 3 distinctly longer than 5
	evansi Matthews
-	Vertex smooth (Fig 7A); metasomal terga 2–3 with sculpture obscured in middle and
	not covering basal 3/4; hind tarsomere 3 equal or shorter than 5 elegans Matthews
11(7).	Ovipositor shorter than metasoma, usually about equal in length to gaster 12
-	Ovipositor equal to or longer than metasoma
12(11).	Vertex smooth and polished (Fig 16A) rubidus (Rossi)
-	Vertex finely striate (Fig 15A) parvulus Matthews
13(11).	Ovipositor at least as long as entire body, occasionally slightly longer scomes Matthews
-	Ovipositor equal to or slightly longer than metasoma
14(13).	Vertex and temples distinctly and strongly rugose-acinose, the rugae usually continuing
	down temple to mandible (Fig 9A); vertex broad, ocellar-occiput distance usually 1.5
	times longer than ocellar-ocular distance floridanus Ashmead
-	Vertex and temples at most weakly striate, rugulose or acinose, often entirely smooth,
	rugae on temples rarely extending to mandibles (Figs 10A, 11A, 12A, 14A, 17A);
	vertex narrower, ocellar-occiput distance at most 1.2 times longer than ocellar-eye
	distance, often equal
15(14).	Forewing weakly infumated and usually without distinct dark transverse bands,
	occasionally with weak indistinct bands (Fig 17E) sequoiae Ashmead
- 1	Forewing with distinct dark transverse bands, rarely these bands weakly infumated 16
16(15).	Vertex narrow, length (ocellar-occipital distance) equal to or less than ocellar-ocular
7	distance (Fig 10A); outer apical margin of hind tibia with 2-3 small spines
	(Fig 10E) impus Matthews

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-	Vertex broader, length greater than ocellar-ocular distance; outer apical margin of hind tibia with 3–6 small spines
17(16).	Mesopleuron with delicately swirled striae above precoxal sulcus (Fig 14B); vertex more or less evenly weakly strigose (Fig 14A); body color yellow pallidus Ashmead
-	Mesopleuron entirely smooth or weakly acinose above precoxal sulcus (Fig 11B, 12B); vertex entirely smooth or weakly strigose anteriorly, usually smooth posteriorly and near eyes (Figs 11A, 12A); body dark honey yellow or brown
18(17). -	Mesopleuron entirely smooth from precoxal sulcus to subalar area (Fig. 12B); vertex entirely smooth (Fig 12A) leiopleuron Marsh and Strazanac, new species Mesopleuron weakly acinose or striate, occasionally smooth directly above precoxal sulcus (Fig 11B); vertex weakly striate medially and anteriorly (Fig 11-A)
Males	
1.	Precoxal sulcus with distinct carina along lower margin extending from epicnemial carina to mid-coxal cavity

1.	Trecoxar suicus with district carria along rower margin exterioring from epichemiai
	carina to mid-coxal cavity
	Precoxal sulcus without a distinct carina along lower margin
2(1).	Fore wing vein 2RS longer than vein 3Rsa
-	Fore wing vein 2RS equal in length, or nearly so, to vein 3Rsa brunneus Ashmead
3(1).	Eyes small, malar space at least 3/4 eye height, often equal 4
-	Eyes larger, malar space at most 1/2 eye height
4(3).	Hind wing with stigma-like swelling at junction of veins SC+R, r-m and R
	(Fig. 18H) stigmatus Matthews
	Hind wing without such stigma-like swelling
5(4).	Scutellum rugose; vertex and temple smooth
-	Scutellum smooth; vertex and temples rugulose
6(5).	Maxillary palpus very short, at most equal to eye height (the unknown male of brevipalpus will presumably run here) brevipalpusMatthews
-	Maxillary palpus longer, usually twice eye height brachyurus Ashmead
7(3).	Petiole long and narrow, at least as long as 1.5 times length of middle femur, usually
	longer, in side view gently sloping toward base
-	Petiole shorter, never longer than 1.5 length of middle femur, in side view strongly arched at base
8(7).	Scutellum smooth and polished longipetiolatus Ashmead
_`´	Scutellum not smooth, usually weakly acinose or acinose
9(8).	Metasomal terga 2–4 distinctly and completely sculptured, lateral margin of terga 2+3
	sharp and distinct its entire length; fore wing vein 3CU interstitial and on same line
	as vein 1CU
-	Metasomal terga 3 and 4 smooth, lateral margin of terga 2+3 sharp only at base; fore
	wing vein 3CU not on same line as vein 1CU, thus vein 2CU present 10
10(9).	Vertex transversely striate, at least directly behind ocelli; metasomal terga 2-3
	completely sculptured on basal 3/4; hind tarsomere 3 distinctly longer than
	5 <i>evansi</i> Matthews
-	Vertex smooth; metasomal terga 2–3 with sculpture obscured in middle and not
	covering basal 3/4; hind tarsomere 3 equal or shorter than 5 elegans Matthews
11(7).	Vertex and temple distinctly and strongly acinose to rugose-acinose, the rugae usually
	continuing down temple to mandible floridanus Ashmead
-	Vertex and temple at most striate, rugulose or acinose, often entirely smooth, rugae on
10/11:	temple rarely extending to mandibles
12(11).	Fore wings hyaline, without distinct dark bands
-	Fore wings with distinct dark bands

13(12).	Frons delicately striate rubidus (Rossi)
-	Frons smooth sequoiae Ashmead
14(12).	Vertex nearly entirely striate or strigate comes Matthews
-	Vertex weakly striate, often smooth near eyes and occipital carina or entirely smooth 15
15(14).	Vertex narrow, ocellar-occipital distance equal or less than ocellar-ocular distance . 16
-	Vertex broader, ocellar-occipital distance greater than ocellar-ocular distance 17
16(15).	Sculpture on metasomal terga 2–3 covering at most basal half impus Matthews
-	Sculpture on metasomal terga 2–3 extending beyond basal half parvulus Matthews
17(15).	Mesopleuron with delicately swirled striae above precoxal sulcus pallidus Ashmead
-	Mesopleuron smooth or weakly acinose above precoxal sulcus
18(17).	Mesopleuron entirely smooth leiopleuron Marsh and Strazanac, new species
-	Mesopleuron weakly acinose above precoxal sulcus laflammei Provancher

### Spathius brachyurus Ashmead (Figs 2 A-H)

Rhopalophorus fasciatus Provancher 1886:129. Preoccupied by Walker 1874.

Spathius abdominalis Riley 1890:350. Nomen nudum.

Spathius brevicaudus Ashmead 1892:258. Nomen nudum.

Spathius brachyurus Ashmead 1893:73; Matthews 1970:26.

Spathius dignus Muesebeck and Walkley 1951:169. New name for fasciatus Ashmead. Synonymized by Matthews 1970.

Female.—Color: body varying from light to dark brown; antenna usually with basal flagellomeres light brown and apical ones dark brown; wings lightly dusky, without distinct bands, with infuscated spots below stigma and along vein 1M. Body size: 3.0-5.5 mm. Head: face rugose or rugose-costate; maxillary palpus about twice eye height; frons rugose; vertex and temple rugulose costate; eyes small, malar space slightly less that eye height, temple about equal to eye width; vertex broad, ocellar-occipital distance slightly greater than ocellar-ocular distance; antenna with 19-25 flagellomeres, those beyond first subcubical, only slightly longer than wide. Mesosoma: propleuron rugose; pronotum rugose, costate above fore coxa, propleural groove wide with widely spaced cross carinae; mesoscutal lobes acinose; notauli scrobiculate, meeting at scutellar furrow in triangular rugose area with two distinct longitudinal carinae;

scutellum smooth; mesopleuron rugose in subalar area and above middle coxa, central disc acinose; precoxal sulcus distinctly scrobiculate, about 3/4 length of mesopleuron; propodeum rugose, apical lateral corners distinctly produced, median carina and areola distinct, areola with several cross carinae. Wings: fore wing vein 2RS nearly as long as vein 3RSa, vein 3CU not on same line as vein 1CU, small section of vein 2CU present; hind wing vein r-m slightly less than 1/2 length of vein 1M. Legs: fore tibia with irregular single row of 12-15 spines along anterior edge; hind tibia with 3-4 spines at outer apical lobe; hind coxa with distinct antero-ventral tooth at base. Metasoma: petiole arched at base in lateral view, rugose dorsally on basal half, longitudinally carinate on apical half; remainder of terga smooth, with single transverse row of setae at apex of each tergum; ovipositor as long as metasoma.

Male.—Essentially as in female; antenna slender, flagellomeres distinctly longer than wide.

Distribution.—Quebec south to South Carolina, west to Wisconsin and Texas, California. The California specimens are definitely this species which would indicate brachyurus probably occurs throughout North America.

Biology.—This species has been recorded attacking *Pissodes strobi* (Peck) and *P. approximates* Hopkins (Coleoptera: Curculionidae) in pine (Pinaceae; *Pinus*) and

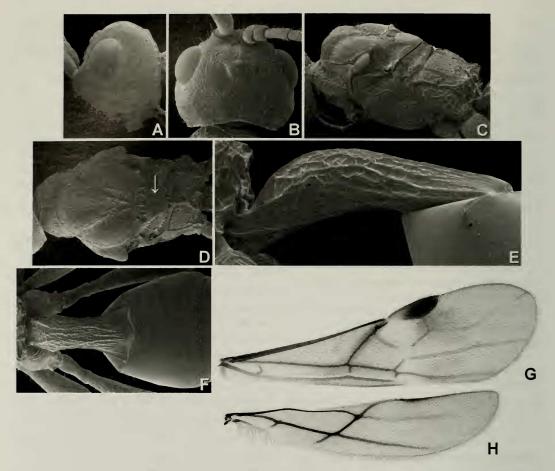


Figure 2. *Spathius brachyurus* Ashmead, female. A, head lateral view; B, head dorsal view; C, mesosoma lateral view; D, mesosoma dorsal view with scutellum indicated; E, petiole lateral view; F, petiole and metasoma terga 2+3 dorsal view; G, fore wing; H, hind wing.

Dryocoetes autographus (Ratzeburg) (Coleoptera: Scolytidae) in spruce (Pinaceae: Picea). The specimens from California are labeled "Galleries of Steremnius carinatus and Hylastes nigrinus in Pseudotsuga menziesii."

Comments.—This species and brevipalpus are distinctive by the small eye and by the apical lateral corners of the propodeum being protuberant. It can be separated from brevipalpus by the longer maxillary palpus and the single transverse row of setae at apex of each metasomal tergum.

## Spathius brevipalpus Matthews (Fig 3A)

Spathius brevipalpus Matthews 1970:29.

Female.—Color: body entirely honey yellow; hind tibia without basal white band; fore wing lightly infuscated, without distinct bands. Body size: 3.0-3.5 mm. Head: face rugulose, protruding at antennal insertion so that antennae are inserted on distinct frontal shelf; maxillary palpus short, less than eye height; hypostomal carina distinctly protuberant; frons rugose; vertex and temple rugulose-striate; eyes small, malar space about equal to eye height, temple slightly greater than eye width; vertex broad, ocellar-occipital distance greater than ocellar-ocular distance; antenna with 19-20 flagellomeres, those beyond first subcubical, only slightly longer than wide. Mesosoma: propleuron ru-

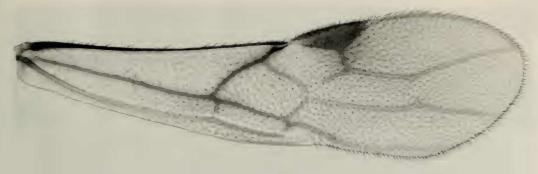


Figure 3. Spathius brevipalpus Matthews, female. A, fore wing.

gulose; pronotum carinate-rugulose, pronotal groove weakly scrobiculate, nearly smooth; mesoscutal lobes acinose, notauli scrobiculate, meeting before scutellar furrow in shallow rugose area; scutellum smooth, flat; mesopleural disc acinoserugulose, subalar area coarsely rugose; precoxal sulcus shallow, with weak cross carinae; propodeum with apical-lateral corners strongly produced, rugulose laterally and at basal areas, all propodeal carina distinct, areola with several cross carinae. Wings: fore wing vein 2RS about 2/3 length of vein 3RSa, vein 3CU not on same line as vein 1CU, small section of vein 2CU present; hind wing vein r-m about 1/2 length of vein 1M. Legs: fore tibia with irregular row of about 15 spines along anterior edge; hind tibia with 3 spines at outer apical rim; hind coxa with distinct antero-ventral tooth at base. Metasoma: petiole distinctly arched at base in lateral view, rugulose dorsally at base, longitudinally costate on apical half; all remaining terga smooth and polished, each with two or three transverse rows of long setae; ovipositor about as long as metasoma.

Male.—Unknown.

Distribution.—Only known specimens are from North Carolina, South Carolina and Texas.

Biology.—Unknown. One specimen of the type series from North Carolina was labeled as being reared from "Pachylobius picivorous" which has not been confirmed. Comments.—This species and brachyurus are distinctive by their small eyes and by the propodeum with apical lateral corners produced; brevipalpus can be separated from brachyurus by the very short maxillary palpi and the multiple transverse rows of setae on the metasomal terga.

### Spathius brunneus Ashmead (Figs 4 A-I)

Spathius brunneus Ashmead 1893:72; Matthews 1970:70.

Female.—Color: body light honey yellow or orange, metasomal terga beyond third usually brown, apical flagellomeres darker, hind tibia darker with white band on basal 1/5; wings banded, basal 1/3 of stigma yellow. Body length: 3.0-5.0 mm. Head: face transversely rugulose-striate; frons transversely striate; vertex finely striate anteriorly, diminishing to smooth at occipital carina; temple finely striate to malar mandible; vertex broad, ocellar-occipital distance about twice ocellar-ocular distance; temple about as wide as eye, in dorsal view bulging slightly beyond eye margin; malar space about 1/2 eye height; antenna with 31-34 flagellomeres. Mesosoma: propleuron rugulose, propleural flange smooth; pronotum rugulose-striate, pronotal groove weak and often absent; mesoscutal lobes acinose; notauli weakly scrobiculate, meeting before scutellum in shallow triangular rugose area; scutellum

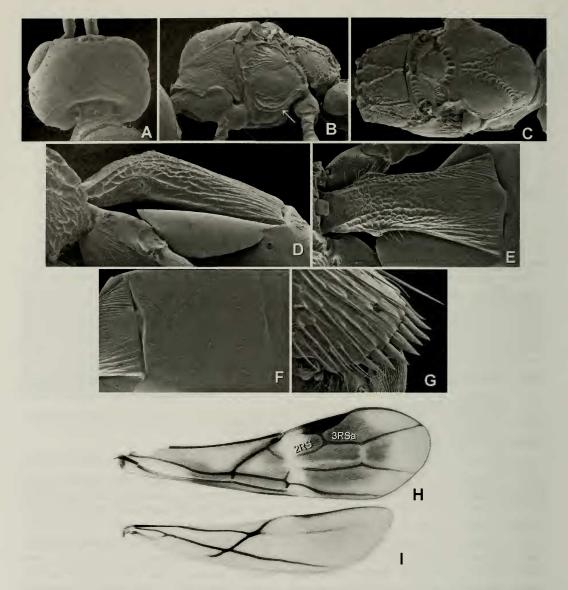


Figure 4. Spathius brunneus Ashmead, female. A, head dorsal view; B, mesosoma lateral view with carina along lower margin of sternalus indicated; C, mesosoma dorsal view; D, petiole lateral view; E, petiole dorsal view; F, metasoma terga 2+3 dorsal view; G, outer apical margin of hind tibia; H, fore wing with 2RS and 3RSa indicated; I, hind wing.

conical, acinose, scutellar furrow with 6–8 cross carinae; mesopleural disc transversely costate dorsally, weakly acinose above precoxal sulcus, subalar area rugose; precoxal sulcus smooth or with longitudinal carinae, bordered below by strongly curved distinct carina; propodeum acinose laterally, dorsal areas rugulose, carina often indistinct, areola rugulose. Wings:

fore wing vein 2RS about equal in length to vein 3RSa, vein 3CU not interstitial with vein 1CU, thus small section of vein 2CU present; hind wing vein r-m less than 1/2 length of vein 1M. Legs: fore tibia with 2–3 irregular rows of 30–40 spines along anterior edge; hind tibia with 6–7 spines at outer apical rim; antero-ventral tooth at base of hind coxa weakly pointed. Meta-

soma: petiole sharply arched in side view at base, rugose on basal 1/2, costate on apical 1/2; second tergum weakly striate-acinose at extreme base, remainder of terga smooth and polished, sometimes with very weak transverse band of punctures anterior to setal bands; ovipositor shorter than metasoma.

Male.—Essentially as in female except femora are swollen.

Distribution.—The only known specimens are from Maryland, West Virginia and Florida.

Biology.—This species has been reared from Agrilus fallax Say (Coleoptera: Buprestidae) and Scolytus muticus Say (Coleoptera: Scolytidae) infesting Celtis occidentalis L. (Ulmaceae).

Comments.—This species, along with trifasciatus, are distinguished by the precoxal sulcus which is bordered ventrally by a distinct carina. It can be separated from trifasciatus by its ovipositor which is shorter than the metasoma (longer than the metasoma in trifasciatus), swollen scutellum (flat in trifasciatus), the shallower area on the mesoscutum where the notauli meet, and the lighter body color.

### Spathius calligaster Matthews (Figs 5 A–H)

Spathius calligaster Matthews 1970:35.

Female.—Color: body generally honey yellow to light brown; antenna with scape, pedicel and basal flagellomeres yellow, gradually turning light brown to apex; fore and middle legs including coxae and trochanters yellow, femora and tibiae often darker, hind leg brown except trochanters yellow, hind tibia yellow on apical 1/3 or 1/4; fore wing banded, tegula yellow. Body size: 5.5-7.0 mm. Head: face transversely costate-rugose; frons transversely costate; vertex striate behind ocellae, smooth near occipital carina; temple smooth except weakly striate near eyes; malar space 1/2 eye height, temple slightly less than eye width; vertex broad, ocellar-ocular dis-

tance slightly less than ocellar-occipital distance; antenna with 25-45 flagellomeres. Mesosoma: mesosoma somewhat flattened dorso-ventrally; propleuron rugose; pronotum costate posteriorly, rugose anteriorly, pronotal groove distinctly scrobiculate; mesoscutal lobes coarsely acinose, notauli scrobiculate anteriorly, meeting posteriorly before scutellum in depressed coarsely rugose area; scutellum acinose; mesopleuron longitudinally costate, disc smooth above precoxal sulcus, subalar area rugose, precoxal sulcus distinctly scrobiculate, nearly as long as mesopleuron; propodeum entirely rugose, carinae absent except for short section of median carina. Wings: fore wing vein 2RS distinctly curved, vein 2RS about 1/3 length of vein 3RSa, vein 3CU on same line as vein 1CU; hind wing vein r-m about 1/4 length of vein 1M, vein m-cu distinctly basad of vein r-m. Legs: fore tibia with irregular row of 15-20 spines along anterior edge; hind tibia without spines at apical lobe; hind coxa elongate, acinose, distinct antero-ventral tooth at base. Metasoma: petiole long and slender, about 2/3 length of gaster, evenly sloped to bas in lateral view, nearly entirely rugose dorsally; metasomal terga 2-5 acinose except apical edges smooth; terga 2-3 strongly margined laterally for entire length; ovipositor as long as or longer than entire body.

Male.—Essentially as in female.

Distribution.—Quebec south to South Carolina, west to Illinois and Ohio.

*Biology.*—The only reliable rearing record is from *Melasis pectinicornis* Melsh. (Coleoptera: Eucnemidae).

Comments.—This species is distinctive by its coarsely sculptured gaster, especially terga 2–5, and the absence of spines at the apical lobe of the hind tibia.

### Spathius comes Matthews (Figs 6 A–C)

Spathius comes Matthews 1970:59.

Female.—Color: entire body honey yellow or light brown; legs often lighter, trochan-

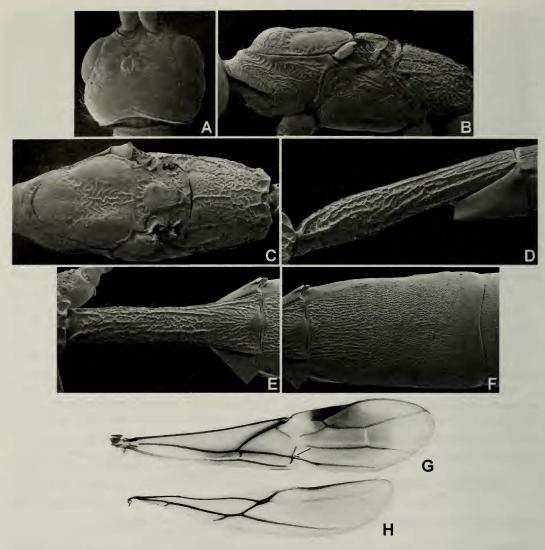


Figure 5. Spathius calligaster Matthews, female. A, head dorsal view; B, mesosoma lateral view; C, mesosoma dorsal view; D, petiole lateral view; E, petiole dorsal view; F, metasoma terga 2+3 dorsal view; G, fore wing with interstitial 2CU vein indicated; H, hind wing.

ters usually yellow; antennae yellow at base, becoming light brown to apex; wings banded, basal 1/3 of stigma yellow. *Body size*: 2.5–5.0 mm. *Head*: face transversely striate-rugulose; frons transversely striate; vertex striate, becoming striate-acinose laterally; temple acinose; vertex broad, ocellar-ocular distance about 2/3 ocellar-occipital distance; malar space 1/2 eye height; antenna with 26–38 flagellomeres. *Mesosoma*: propleuron rugulose, propleural flange broad and smooth along posterior

border; pronotum rugose above and below pronotal groove which is scrobiculate except costate posteriorly; mesoscutal lobes acinose, notauli scrobiculate anteriorly, meeting before scutellum in triangular rugose area; scutellum acinose; propodeum acinose on basal lateral areas and laterally, rugose dorso-laterally, along median carina and at apex, carinae and areola not distinct. Wings: fore wing vein 2RS equal in length to vein 3RSa, vein 3CU not on same line as vein 1CU, short vein 2CU

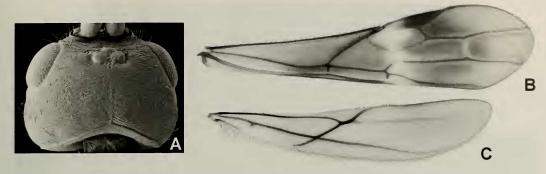


Figure 6. Spathius comes Matthews, female. A, head dorsal view; B, fore wing; C, hind wing.

present; hind wing vein r-m about 2/5 length of vein 1M. Legs: fore tibia with two irregular rows of 15–30 spines along anterior edge; hind tibia with three spines at outer apical lobe; hind coxa acinose, with blunt small antero-ventral tooth at base. Metasoma: petiole distinctly arched at base in lateral view, rugose dorsally except costate at extreme apex; terga 2–3 acinose on basal 1/2, remainder of terga smooth; ovipositor usually as long as entire body, occasionally slightly longer.

Male.—Essentially as in female.

Distribution.—Nova Scotia and Quebec south to Maryland, west to Wisconsin and Ohio.

Biology.—Reared from Chrysobothris pusilla Cast. (Coleoptera: Cerambycidae) in spruce and Melanophila fulvoguttata (Harr.) (Coleoptera: Buprestidae) in hemlock (Pinaceae: Tsuga).

Comments.—This species is similar to floridanus because of the vertex sculpturing but is distinguished by the ovipositor which is as long as or longer than the entire body.

### Spathius elegans Matthews (Figs 7 A–G)

Spathius elegans Matthews 1970:39.

Female.—Color: head and mesosoma usually light brown, occasionally honey yellow, propodeum honey yellow; petiole honey yellow, gaster light brown, apex of third tergum often lighter; antenna yellow,

becoming light brown apically; legs honey yellow, fore and mid coxae and trochanters and hind trochanters yellow, hind tibia with white or yellow band on basal 1/4-1/ 5; wings banded, basal 1/3 of stigma yellow. Body size: 3.5-7.0 mm. Head: face and frons transversely striate; vertex smooth; temple smooth, occasionally weakly acinose behind eye; malar space 1/2 eye height; temple about equal to eye width; vertex broad, ocellar-occiput distance about 1.5 times ocellar-ocular distance; antenna with 30-40 flagellomeres. Mesosoma: propleuron rugose; pronotum rugose, propleural groove scrobiculate-rugose; mesoscutal lobes acinose, notauli scrobiculate, meeting posteriorly in excavated triangular rugose area with two converging distinct longitudinal carinae; scutellum acinose; mesopleural disc acinose-rugulose, subalar area coarsely rugose, precoxal sulcus scrobiculate, about 2/3 length of mesopleuron; propodeum acinose dorsally and laterally, rugose dorso-laterally, median carina and areola distinct. Wings: fore wing vein 2RS equal to or sometimes slightly longer than vein 3RSa, vein 3CU nearly on same line as 1CU; hind wing vein r-m less than 1/2 length of vein 1M. Legs: fore tibia with irregular double row of 25-50 spines along anterior edge; hind tibia with 3-5 spines on outer apical lobe; hind tarsomere 3 slightly shorter than tarsomere 5; hind coxa acinose, with small but distinct antero-ventral tooth at base. Metasoma: petiole long and

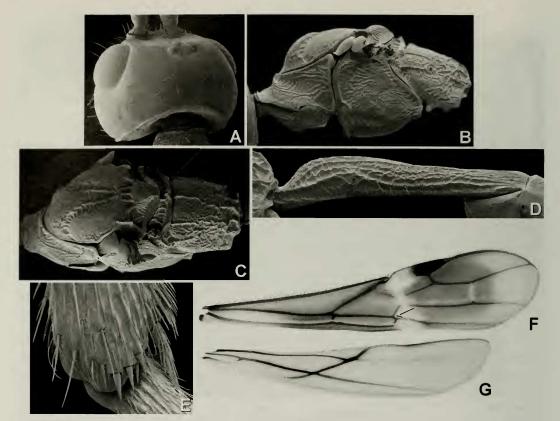


Figure 7. Spathius elegans Matthews, female. A, head dorsal view; B, mesosoma lateral view; C, mesosoma dorsal view; D, petiole lateral view; E, outer apical margin of hind tibia; F, fore wing; G, hind wing.

slender, about 3/4 length of mesosoma, dorsally rugulose; second metasomal tergum acinose, third tergum weakly acinose laterally and usually smooth medially; remainder of terga smooth; ovipositor about as long as entire body.

Male.—Essentially as in female.

Distribution.—This is perhaps the most widely collected species and occurs throughout North America.

Biology.—In spite of the many specimens studied, there are no accurate host records. The species has been reared from maple Aceraceae: Acer), beech (Betulaceae: Betula) and hickory (Juglandaceae: Carya) and has been associated with powderposted wood infested with Hadrobregmus (Coleoptera: Anobiidae).

Comments.—This species is similar to evansi but is distinguished by the smooth vertex, less sculptured metasomal terga 2-

3, and the third hind tarsomere shorter than the fifth tarsomere.

#### Spathius evansi Matthews (Figs 8 A-H)

Spathius evansi Matthews 1970:42.

Female.—Color: body generally entirely honey yellow or light brown; fore and mid coxae and trochanters and hind trochanters lighter yellow, hind tibia with yellow band on basal 1/4; antenna becoming light brown apically; wings banded, stigma yellow on basal 1/3. Body size: 3.5–9.0 mm. Head: face and frons transversely costate; vertex transversely costate or striate at least behind ocelli and near eyes, often on entire vertex; temple smooth, occasionally weakly striate near mandible; malar space slightly less than 1/2 eye height; temple equal to eye width; antenna

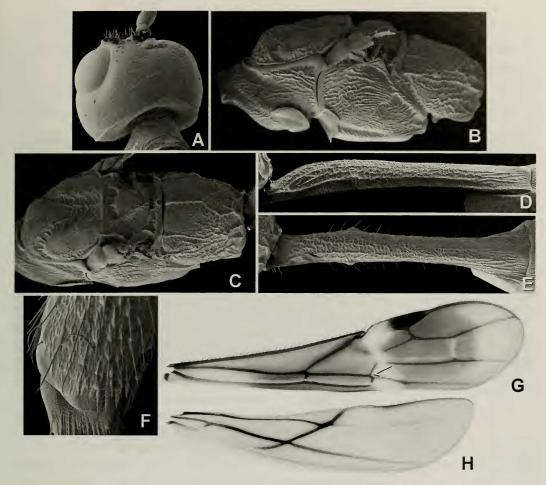


Figure 8. *Spathius evansi* Matthews, female. A, head dorsal view; B, mesosoma lateral view; C, mesosoma dorsal view; D, petiole lateral view; E, petiole dorsal view; F, outer apical margin of hind tibia; G, fore wing with 2CU indicated; H, hind wing.

with 35-50 flagellomeres; temple broad, ocell-occiput distance about 1.5 times ocellar-ocular distance. Mesosoma: propleuron acinose posteriorly, rugulose anteriorly; pronotum rugose medially and dorsally, acinose ventrally and over pronotal collar, pronotal groove distinctly scrobiculate, obscured posteriorly; mesoscutal lobes acinose, notauli scrobiculate, meeting posteriorly in deeply excavated triangular rugose area; scutellum acinose; mesopleural disc acinose above precoxal sulcus, transversely costate dorsally and posteriorly, subalar area often rugose; precoxal sulcus distinctly scrobiculate, about 2/3 length of mesopleuron; propodeum aci-

nose apically and laterally, rugose apically and along dorsal lateral edge, basal carina and areola usually distinct, often weakly indicated. Wings: fore wing vein 2RS about as long as vein 3RSa, vein 3CU not on same line as vein 1CU so that short section of vein 2CU present; hind wing vein r-m less than half length of vein 1M. Legs: fore tibia with irregular double row of 25-35 spines along anterior edge; hind tibia with 2-5 spines at outer apical lobe; hind tarsomere 3 usually distinctly longer than tarsomere 5; hind coxa acinose, with distinct sharply pointed antero-ventral tooth at base. Metasoma: petiole long and narrow, nearly as long as mesosoma, rugulose-acinose dorsally; terga 2–3 distinctly and evenly acinose on basal 3/4, apical 1/4 smooth; remainder of terga smooth; ovipositor longer than entire body, usually twice as long as fore wing.

Male.—Essentially as in female.

Distribution.—Quebec south to Florida, west to Wyoming and New Mexico. Probably occurs throughout North America.

*Biology.*—No hosts have been recorded and we have not seen any reared specimens.

Comments.—This species is very similar to elegans but can be distinguished by its striate vertex (smooth in elegans), the metasomal terga 2–3 being sculptured on basal 3/4 (elegans has a smooth area medially), and third hind tarsomere being longer than the fifth (shorter in elegans).

### Spathius floridanus Ashmead (Figs 9 A–I)

Spathius floridanus Ashmead 1893:71; Matthews 1970:75.

Spathius simillimus Ashmead 1893:73; Matthews 1970:72. New synonymy.

Female.—Color: body honey yellow or light brown, apical terga of metasoma often brown; hind tibia with white band at basal 1/6; antenna yellow basally, becoming light brown to apex; wings distinctly banded. Body size: 1.5-4.5 mm. Head: face transversely rugulose-costate; vertex transversely costate-acinose, often becoming acinose near and behind eye; frons rugulose or transversely rugulose-costate; temple and malar space acinose; vertex broad, ocellar-ocular distance 2/3 ocellar-occipital distance; temple bulging slight beyond eye margin in lateral view; malar space about 1/2 eye height; antenna with 25-40 flagellomeres. Mesosoma: propleuron rugulose, occasionally acinose on propleural flange; pronotum longitudinally costate behind and above pronotal groove, before groove often acinose or costate-acinose; pronotal groove distinctly scrobiculate; mesoscutal lobes acinose; notauli strongly scrobiculate anteriorly, meeting posteriorly in triangu-

lar depressed rugose area; scutellum acinose; mesopleural disc strongly longitudinally costate dorsally, costae becoming weaker near precoxal sulcus and often acinose just above precoxal sulcus, which is scrobiculate; subalar area rugose; propodeum rugulose with distinct basal carinae and areola, basal lateral areas often acinose, lateral area often acinose. Wings: fore wing vein 2RS equal to or slightly shorter than vein 3RSa, vein 3CU not on same line as vein 1CU, thus small segment of vein 2CU present; hind wing vein r-m less than half length of vein 1M. Legs: fore tibia with irregular single or double row of 15-25 spines along anterior edge; hind tibia with 2-6 spines on outer apical lobe; hind coxa with small but distinct antero-ventral tooth at base. Metasoma: petiole arched at base in lateral view, dorsally rugose at base, longitudinally costate at apex; gastral tergum 2 weakly acinose or strigate at base, often nearly entirely smooth, remainder of gastral terga smooth; terga 4-6 occasionally with a weakly defined transverse punctate band anterior to row of setae; ovipositor equal to or slightly longer than metasoma.

Male.—Essentially as in female.

Distribution.—New Brunswick south to Florida, west to Ontario, Wisconsin and Texas.

Biology.—Recorded hosts are: Agrilus anxius Gory, A. bilineatus (Weber), Chrysobothris femorata (Oliv.) (Coleoptera: Buprestidae); Magdalis olyra (Herbst) (Coleoptera: Curculionidae); Phymatodes aereum (Newman), Xylotrechus colonus (F.) (Coleoptera: Cerambycidae). In addition, we have seen specimens of floridanus reared from galleries of Agrilus planipennis, the emerald ash borer, from Michigan.

Comments.—Matthews (1970) based his separation of simillimus from floridanus primarily on the presence of a transverse punctate band on gastral terga 4–6 anterior to the transverse row of setae. Our examination of several hundred specimens has shown a wide variation of this band from distinct to absent. This variation, including

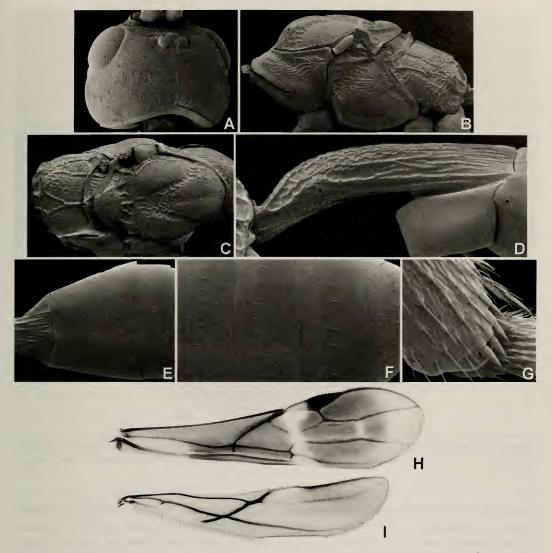


Figure 9. *Spathius floridanus* Ashmead, female. A, head dorsal view; B, mesosoma lateral view; C, mesosoma dorsal view; D, petiole lateral view; E, metasoma terga 2+3, and 4 dorsal view; F, metasoma terga 4, 5, 6, and 7 dorsal view; G, outer apical margin of hind tibia; H, fore wing; I, hind wing.

the wide overlap in number of spines at the apical lobe of the hind tibia and the wide variation in sculpture of the mesopleural disc, has convinced us that *simillimus* and *floridanus* are the same species. The name *floridanus* is chosen because of its page preference in Ashmead's original publication (Ashmead 1893).

### Spathius impus Matthews (Figs 10 A-G)

Spathius impus Matthews 1970:56.

Female.—Color: body honey yellow, apical half of metasoma usually light brown, legs lighter yellow; wings banded; antenna yellow basally, gradually becoming light brown to apex. Body size: 1.5–3.5 mm. Head: face weakly rugulose-striate; frons striate; vertex strigate; temple smooth, occasionally weakly acinose near occipital carina; malar space 1/2 eye height; vertex narrow, ocellar-occular distance about equal to ocellar-occipital distance; antenna with 20–30 flagellomeres. Mesosoma: propleuron

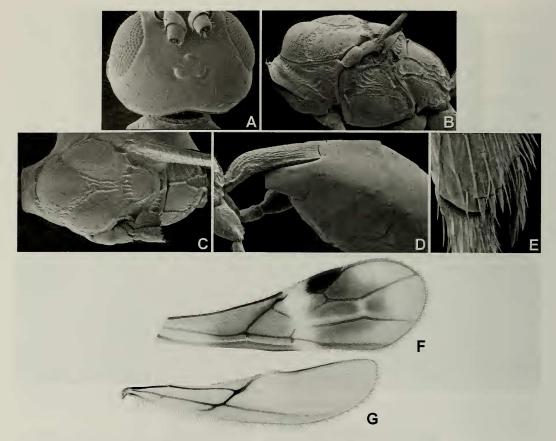


Figure 10. Spathius impus Matthews, female. A, head dorsal view; B, mesosoma lateral view; C, mesosoma dorsal view; D, petiole and metasoma lateral view; E, outer apical margin of hind tibia; F, fore wing; G, hind wing.

rugulose; pronotum rugulose, pronotal groove scrobiculate but weakly or not at all impressed; mesoscutal lobes acinose; notauli scrobiculate anteriorly, meeting before scutellum in narrow triangular rugose area, often with two distinct short longitudinal carinae; scutellum acinose; mesopleural disc acinose, becoming longitudinally costulate dorsally, subalar area costate; precoxal sulcus scrobiculate, only weakly impressed; propodeum distinctly acinose dorsally and laterally, areola and basal carina distinct. Wings: fore wing vein 2RS slightly longer than vein 3RSa, vein 3CU nearly on same line as vein 1CU, occasionally very short segment of vein 2CU present; hind wing vein r-m about 1/3 length vein 1M. Legs: fore tibia with

irregular row of about 15 spines along anterior edge; hind tibia with 3–4 spines at outer apical lobe. *Metasoma*: petiole arched at base in lateral view, dorsally rugose on basal half, costate on apical half; second tergum weakly acinose on basal half, remainder smooth; remainder of terga smooth; ovipositor equal to or slightly longer than metasoma.

Male.—Essentially as in female.

Distribution.—Quebec south to Florida, west to Michigan and Louisiana.

*Biology.*—Reared from *Phloeosinus canadensis* Swaine and *P. dentatus* (Say) (Coleoptera: Scolytidae) in red cedar (Cupressaceae: *Juniperus*).

Comments.—This species is similar to parvulus but is distinguished by the ovi-

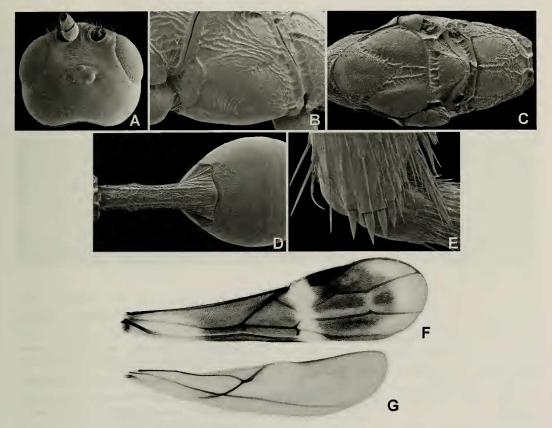


Figure 11. Spathius laflammei Provancher, female. A, head dorsal view; B, mesopleuron; C, mesosoma dorsal view; D, petiole and metasoma terga 2+3 dorsal view; E, outer apical margin of hind tibia; F, fore wing; G, hind wing.

positor being as long as or longer than the metasoma (shorter than the metasoma in *parvulus*); it is also similar to *pallidus* but is distinguished by the narrower vertex (broader in *pallidus*).

### Spathius laflammei Provancher (Figs 11 A-G)

Spathius laflammei Provancher 1880: 164; Matthews 1970:64.

Spathius benefactor Matthews 1970:61. New synonymy.

Female.—Color: body dark honey yellow to brown, petiole and base of gaster often lighter; antenna yellow, becoming darker apically; legs honey yellow, trochanters often lighter, hind tibia with basal 1/4–1/5 yellow or white; wings banded. Body

length: 2.5-6.00 mm. Head: face transversely striate; frons delicately transversely striate; vertex weakly transversely striate medially, becoming smooth near eyes and occiput, occasionally entirely smooth; temple smooth dorsally, often weakly acinose near malar space; vertex broad, ocellar-ocular distance about 2/3 ocellar-occipital distance; malar space slightly less than 1/2 eye height; antenna with 30-45 flagellomeres. Mesosoma: propleuron rugulose; pronotum rugulose dorsally and ventrally, porcate along posterior border at end of pronotal groove which is strongly scrobiculate; mesoscutal lobes acinose; notauli scrobiculate anteriorly, meeting before scutellum in depressed triangular rugose area, often with two distinct longitudinal carinae; scutellum acinose; mesopleuron

smooth or weakly acinose directly above precoxal sulcus, longitudinally costate dorsally and along posterior border, subalar area rugose; precoxal sulcus distinctly scrobiculate; propodeum rugulose dorsally, rugose laterally and apically, basal carina and areola usually distinct but often obscured, areola usually narrow and much longer than wide. Wings: fore wing vein 3RSa equal to or slightly longer than vein 2RS, vein 3CU not on same line as vein 1CU, short section of vein 2CU present; hind wing vein r-m about 1/3 length of vein 1M. Legs: fore tibia with two irregular rows of 20-40 spines along anterior edge; hind tibia with 3-8 spines on outer apical lobe. Metasoma: petiole arched at base in lateral view, shorter than gaster, rugose basally and becoming longitudinally costate-rugose apically; terga 2-3 acinose on basal 1/3-1/2, remainder smooth; remainder of terga smooth and polished; ovipositor slightly longer than metasoma.

Male.—Essentially as in female.

Distribution.—Occurs throughout North America.

Biology.—As mentioned by Matthews (1970), this species has been studied extensively under the name canadensis and he stated that all references to Spathius reared from elm (Ulmaceae: Ulmus) actually refer to benefactor. The following hosts have been recorded for benefactor and laflammei: Hylurgopinus rufipes (Eichh.), Leperisinus aculeatus (Say), Scolytus multistriatus (Marsham) and S. rugulosus Ratz. (Coleoptera: Scolytidae); Magdalis armicollis (Say), M. barbita (Say), M. inconspicua Horn, M. olyra (Coleoptera: Curculionidae); Saperda tridentata Oliv. (Coleoptera: Cerambycidae).

Comments.—We have seen most of the specimens that Matthews studied for his descriptions of benefactor and laflammei and have concluded they represent one highly variable species. There is considerable overlap in the ranges of characters mentioned by Matthews, such as number of teeth on the outer lobe of the hind tibia and number of antennomeres, and it was

difficult to place most specimens in one or the other species. Matthews even hinted at this in his description of benefactor by stating "Larger individuals are superficially similar to laflammei...." We found this to be true with all size specimens and thus have considered benefactor to be a synonym of laflammei. This species is close to pallidus but can be distinguished by the smooth or weakly acinose mesopleuron above the precoxal sulcus (swirled striae in pallidus) and the nearly smooth vertex (weakly but evenly striate in pallidus).

#### Spathius leiopleuron Marsh and Strazanac, new species (Figs 12 A-G)

Female.—Color: head light brown, antennae yellow at base, gradually turning brown to apex; mesosoma light brown, pronotum dark brown anteriorly, mesoscutal lobes often dark brown, metascutum dark brown, mesopleuron occasionally darker dorsally, propodeum occasionally dark brown; petiole light brown, remainder of metasomal terga dark brown; wings distinctly banded, veins dark brown, basal fourth of stigma bright yellow; all coxae and trochanters honey yellow, femora and tibiae brown, tibiae with bright yellow band at base, tarsi light brown. Body size: 3.0-4.5 mm. Head: face transversely costate; frons distinctly depressed, weakly transversely striate; vertex and temple entirely smooth and polished; malar space 1/3 eye height; temple slightly less than eye width; vertex broad, ocellar-occipital distance slightly greater than ocellar-ocular distance; antenna with 24-30 flagellomeres. Mesosoma: propleuron transversely striate; pronotum rugose-striate below pronotal groove, costate above, pronotal groove wide and distinctly scrobiculate; mesoscutal lobes acinose, notauli deeply scrobiculate, meeting posteriorly in deeply depressed triangular rugose area with two distinct longitudinal carinae; scutellum weakly acinose, occasionally smooth; me-

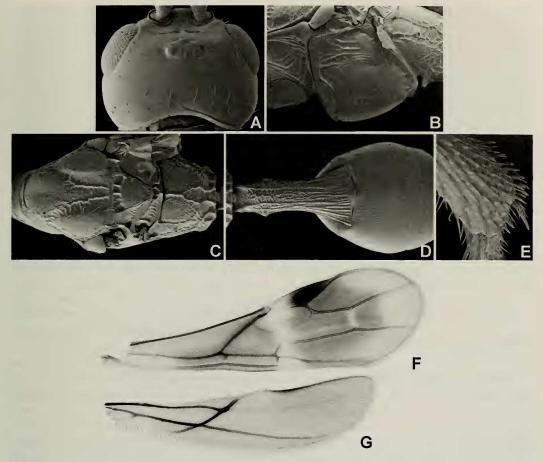


Figure 12. Spathius leiopleuron Marsh and Strazanac, new species, female. A, head dorsal view; B, mesopleuron; C, mesosoma dorsal view; D, petiole and metasoma terga 2+3 dorsal view; E, outer apical margin of hind tibia; F, fore wing; G, hind wing.

sopleuron entirely smooth except for longitudinally carinate subalar area, precoxal sulcus weakly scrobiculate; propodeum rugulose with distinct median carina, areola and lateral carinae, areola transversely costate. Wings: fore wing veins 3RSa and 2RS equal in length, vein 3CU not on same line as vein 1CU, short section of vein 2 CU present; hind wing vein r-m 1/3 length of vein 1M. Legs: fore tibia with 2-3 irregular rows of 25-30 spines along anterior edge; hind tibia with 3-4 spines at outer apical lobe; hind coxa with distinct antero-ventral tooth at base. Metasoma: petiole arched at base in lateral view, coarsely longitudinally rugose-costate dorsally; second tergum entirely acinose; third

tergum punctate across basal 1/3, remainder smooth; remainder of terga smooth, terga 4–6 occasionally with transverse punctate band at base; ovipositor slightly longer than metasoma.

*Male.*—Essentially as in female; body size 2.0–3.5 mm.

Holotype female.—USA: Maryland, Montgomery Co., 4 mi. southwest Ashton, 39°06′36N, 77°01′30W, iii.04 em. iv-v 2004, M. Gates; Reared from dead *Prunus* infested with Coleoptera. Deposited in U. S. National Museum of Natural History, Washington, DC.

Paratypes.—8 females, 12 males, same data as holotype; 1 female, same locality as holotype, 19.viii.03, Gates/Hevel, on dead

Prunus (Rosaceae) infested with scolytids/cerambycids; 1 female, same locality as holotype, 24.viii.03, E. Grissell, on dead Prunus infested with scolytids/cerambycids. Deposited in U. S. National Museum of Natural History, Washington, DC, and Department of Plant and Soil Sciences/Entomology, West Virginia University.

*Biology*.—Unknown. Type series indicates host is a wood boring beetle, probably a scolytid or cerambycid.

Comments.—This species is characterized by the entirely smooth mesopleuron which will distinguish it from all other species.

Etymology.—The species name is from the Greek *leios*, meaning smooth, and the Greek *pleura*, meaning side, in reference to the smooth mesopleuron.

#### Spathius longipetiolatus Ashmead

Spathius longipetiolatus Ashmead 1893:70; Matthews 1970:38.

Matthews (1970:38) prepared a complete description of the two male specimens available at that time. No further specimens, including females, have been discovered and the reader is referred to Matthews for the description. This species is distinctive by the smooth scutellum, elongate petiole, and strongly striate vertex.

### Spathius marshi Matthews (Figs 13 A-H)

Spathius marshi Matthews 1970:30.

Female.—Color: head honey yellow, malar space often lighter; scape. Pedicel and basal flagellomeres honey yellow, flagellum becoming brown to apex; mesosoma honey yellow to light brown; metasoma honey yellow to light brown, apical terga often lighter; legs light brown, hind tibia without basal yellow band; wings lightly dusky without distinct bands, stigma brown with indistinct basal yellow spot. Body size: 2.5–3.5 mm. Head: face, including clypeus, transversely costate; frons transversely costate; vertex and temple smooth;

eye small, malar space equal to eye height; temple slightly wider than eye width; vertex broad, ocellar-occiput distance about equal to ocellar-ocular distance; antenna with 22-24 flagellomeres. Mesosoma: propleuron rugose with several distinct carinae; pronotum rugose, propleural groove distinct, very broad and deep, broadly scrobiculate; mesoscutal lobe rugose, acinose medially; notauli wide and deeply scrobiculate; scutellum rugose, scutellar furrow with median distinct cross carina and often smaller and less distinct carinae laterally; mesopleural disc smooth, subalar area rugose; precoxal sulcus wide and deep, smooth, divided into two or three foveae by one or two cross carinae, extending to mid coxa as distinct longitudinal carina; propodeum rugose, with distinct basal carinae, areola and lateral carinae, apical lateral areas slightly protuberant. Wings: fore wing vein 2RS about 2/ 3 length of vein 3RSa, vein 3CU nearly on same line as vein 1CU; hind wing vein r-m about 1/4 length of vein 1M. Legs: fore tibia with irregular row of 20-25 spines along anterior edge; hind tibia with three spines at outer apical rim; hind coxa with distinct antero-ventral tooth at base. Metasoma: petiole distinctly arched at base in lateral view, rugose dorsally on basal half, apical half longitudinally carinate; remainder of terga smooth; ovipositor slightly longer than metasoma.

*Male.*—Essentially as in female; precoxal sulcus often without cross carinae.

Distribution.—Quebec south to South Carolina, west to Wisconsin and Kansas.

Biology.—Unknown.

Comments.—This species is easily distinguished from the other North American species by its rugose scutellum and mesoscutum, by the small eyes, and by the unique shape of the precoxal sulcus.

### Spathius pallidus Ashmead (Figs 14 A-D)

Spathius pallidus Ashmead 1893: 74; Matthews 1970:53.

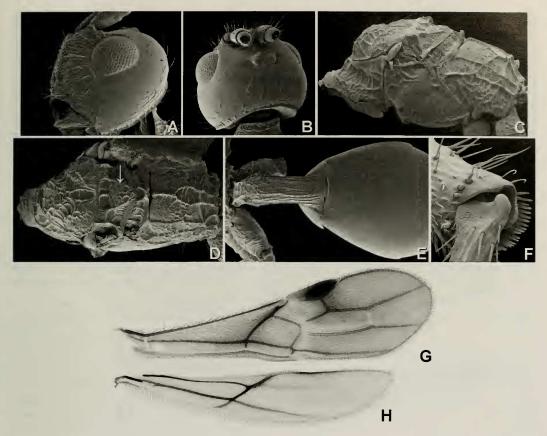


Figure 13. Spathius marshi Matthews, female. A, head lateral view; B, head dorsal view; C, mesosoma lateral view; D, mesosoma dorsal view; E, petiole and metasoma terga 2+3 dorsal view; F, outer apical margin of hind tibia; G, fore wing; H, hind wing.

Female.—Color: body generally light honey yellow, apical segments of metasoma often darker; antenna yellow, gradually darkening toward apex; trochanters of all legs usually yellow, hind tibia with yellow band on basal 1/3; wings banded. Body size: 2.0-3.0 mm. Head: face transversely striate-rugulose; frons transversely striate; vertex transversely striate, becoming acinose or smooth near eye; temple smooth along eye, occasionally acinose near occipital carina; malar space slightly less than eye height; vertex somewhat broad, ocellar-ocular distance slightly shorter than ocell-occiput distance; antenna with 25-35 flagellomeres. Mesosoma: propleuron rugulose except flange usually smooth; pronotum striate or striate-rugulose above groove, acinose below, pronotal groove

indistinctly scrobiculate; mesoscutal lobes acinose; notauli scrobiculate anteriorly, meeting before scutellum in narrow triangular rugose area; scutellum acinose; mesopleuron with delicately swirled striae above precoxal sulcus, subalar area porcate; precoxal sulcus scrobiculate; propodeum acinose or acinose-rugulose dorsally and laterally, median carina and areola distinct but occasionally weakly indicated. Wings: fore wing vein 3RSa nearly equal in length to vein 2RS, vein 3CU not on same line as 1CU, thus small section of vein 2CU present; hind wing vein r-m slightly more than 1/3 length of vein 1M. Legs: fore tibia with irregular double row of 18-25 spines along anterior edge; outer apical lobe of hind tibia with 3-5 spines; hind coxa with small but distinct antero-ventral tooth at

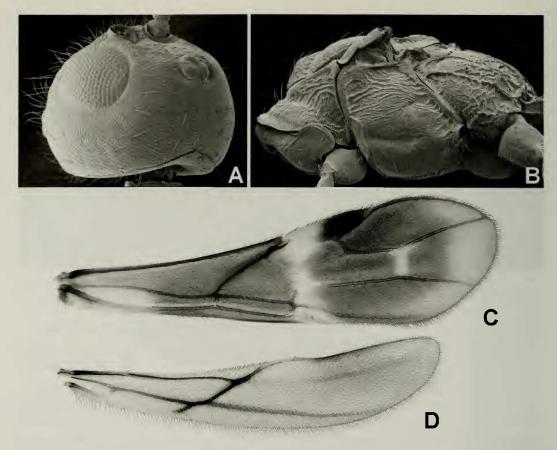


Figure 14. Spathius pallidus Ashmead, female. A, head dorsolateral view; B, mesosoma lateral view; C, fore wing; D, hind wing.

base. *Metasoma*: petiole strongly arched at base in lateral view, rugose dorsally at base, longitudinally striate at apex; metasomal terga 2–3 acinose on basal 1/3, occasionally acinose-striate, remainder smooth; remainder of terga smooth; ovipositor slightly longer than metasoma.

Male.—Essentially as in female.

Distribution.—Ontario and Massachusetts south to Georgia, west to Montana and Texas. We have also seen specimens from Oregon and British Columbia which are apparently this species, indicating the distribution is probably throughout North America.

Biology.—This species has been recorded from the: Dendroctonus frontalis Zimm., Ips avulses (Eichh.), I. grandicollis (Eichh.) (Coleoptera: Scolytidae); Pissodes approximates Hopk., *Phloeosinus dentatus*, *P. nemorensis* Germ. (Coleoptera: Curculionidae).

Comments.—This species is characterized by the delicately swirled striae on the mesopleuron.

### Spathius parvulus Matthews (Figs 15 A–E)

Spathius parvulus Matthews 1970:55.

Female.—Color: body entirely yellow-brown to honey yellow; antenna yellow at base, gradually darkening to brown at apex; wings banded, stigma with white spot on basal 1/4; hind tibia with white band at basal 1/5. Body size: 2.5–3.5 mm. Head: face transversely striate-rugulose; frons weakly transversely striate; vertex weakly transversely striate, the striae often

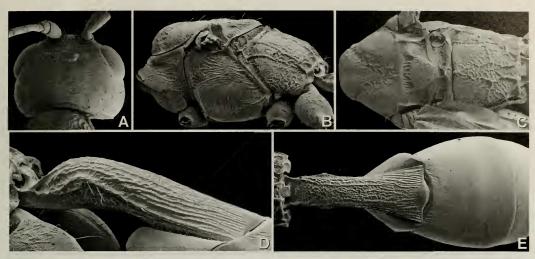


Figure 15. Spathius parvulus Matthews, female. A, head dorsal view; B, mesosoma lateral view; C, mesosoma dorsal view; D, petiole lateral view; E, petiole and metasoma terga 2+3 dorsal view.

curved toward ocelli; temple usually smooth; malar space about 1/3 eye height; temple less than eye width; vertex narrow, ocellar-ocular distance equal to ocellaroccipital distance; antenna with 21-29 flagellomeres. Mesosoma: propleuron rugulose; pronotum rugose dorsally and ventrally, pronotal groove distinctly scrobiculate; mesoscutal lobes acinose; notauli scrobiculate, meeting at scutellum in narrow triangular rugose area with two short longitudinal carinae evident; scutellum acinose; mesopleural disc delicately transversely striate, often smooth above precoxal sulcus, subalar area rugose; precoxal sulcus distinctly scrobiculate; propodeum with basal carina and areola distinct, basal lateral area acinose, lateral areas rugulose. Wings: fore wing vein 2RS about as long as vein 3RSa, vein 3CU not on same line as vein 1CU; hind wing vein r-m less than 1/2 length of vein 1M. Legs: fore tibia with single row of 15-20 spines along anterior edge; outer apical lobe of hind tibia with 3 spines; hind coxa with small distinct antero-ventral tooth at base. Metasoma: petiole strongly arched at base in lateral view, dorsally rugose on basal half, longitudinally rugose-carinate on apical half; terga 2-3 acinose on basal 2/3, remainder

of terga smooth; ovipositor about as long as gaster.

Male.—Essentially as in female.

Distribution.—In the original description, Matthews states that the species occurs in New Mexico, Colorado and South Dakota. He also had specimens tentatively placed in parvulus from the eastern U. S. We have seen these specimens and others in the National Museum collection and they agree with the description. Thus, parvulus probably occurs throughout North America.

Biology.—The type series from New Mexico was reared from *Ips* species in ponderosa pine (Pinaceae: *Pinus ponderosa* C. Lawson). A few specimens from Massachusetts were labeled as being reared from *Pissodes strobi*.

Comments.—This species is similar to rubidus with their short ovipositor, but parvulus differs in its striate vertex. The narrow vertex is also similar to impus but parvulus has a much shorter ovipositor.

### Spathius rubidus (Rossi) (Figs 16 A–G)

Ichneumon rubidus Rossi 1794:110. Spathius rubidus (Rossi): Nees 1834:14; Nixon, 1943:200; Belokobyl'skij 1998:107.

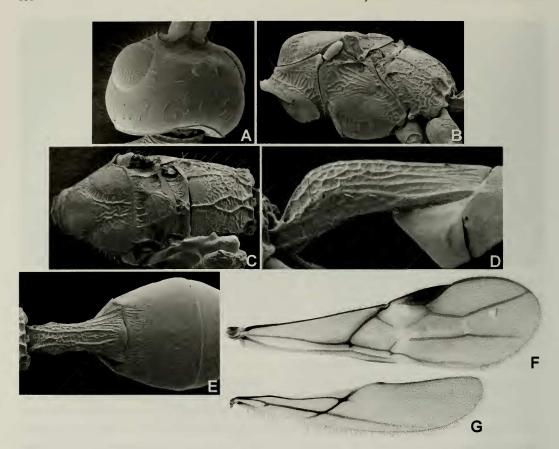


Figure 16. Spathius rubidus (Rossi), female. A, head dorsal view; B, mesosoma lateral view; C, mesosoma dorsal view; D, petiole lateral view; E, petiole and metasoma terga 2+3 dorsal view; F, fore wing; G, hind wing.

Spathius aphenges Matthews 1970:51. New synonymy.

Female.—Color: body light brown to brown; legs yellow; antenna yellow, flagellum gradually darkening to brown at apex; wings not distinctly banded, with darker areas below stigma and in first discal and first subdiscal cells, stigma brown with basal 1/4 yellow. Body size: 2.5-3.5 mm. Head: face finely transversely striate; frons broadly impressed, transversely striate; vertex and temple smooth; malar space about 1/2 eye height; vertex broad, ocellarocular distance 3/4 ocellar-occiput distance; antenna with 23-29 flagellomeres. Mesosoma: propleuron rugulose; pronotum rugose above and below propleural groove which is wide, distinctly scrobiculate and extends to posterior border of pronotum; mesoscutal lobes acinose; notauli scrobiculate, meeting before scutellum in slightly depressed triangular rugose area with two distinct converging longitudinal carinae; acinose; mesopleural disc scutellum smooth, subalar area distinctly rugose; precoxal sulcus scrobiculate; propodeum rugulose, lateral carinae distinct, median carina and areola distinct. Wings: fore wing veins 2RS and 3RSa about equal in length, vein 3CU not on same line as vein 1CU, small section of vein 2CU present; hind wing vein r-m slightly more than 1/3 length of vein 1M. Legs: fore tibia with single row of 10-20 spines along anterior edge; outer apical lobe of hind tibia with 5 spines; hind coxa weakly acinose, with distinct antero-ventral tooth at base. Metasoma: petiole strongly arched basally in lateral view, rugose dorsally on basal 2/3,

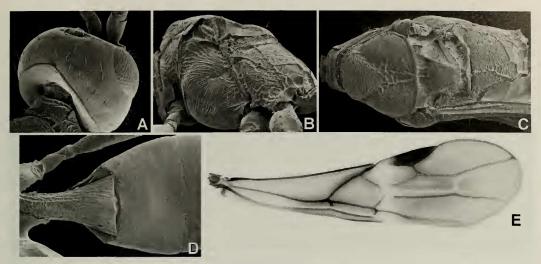


Figure 17. Spathius sequoiae Ashmead, female. A, head dorsal view; B, mesosoma lateral view; C, mesosoma dorsal view; D, petiole and metasoma terga 2+3 dorsal view; E, fore wing.

apical 1/3 longitudinally costate; metasomal terga 2–3 acinose, more weakly so on terga 3 and with posterior edge smooth; remainder of terga smooth; ovipositor shorter than metasoma, usually about equal in length to gaster.

Male.—Essentially as in female.

Distribution.—Yukon Territory south to Texas, west to British Columbia and California; Europe.

Biology.—This species has been reared from a wide variety of scolytids and cerambycids in Europe. In North America it has been reared from Conopthorus coniperda (Schwarz), Ips latidens (Lec.), Phloeotribus lecontei Schedl, and Scolytus abietis Blkm. (Coleoptera: Scolytidae).

Comments.—We have seen authentically identified specimens of Spathius rubidus in the Natural History Museum, London, and there is no question that aphenges is the same species. Spathius rubidus is distinctive by its short and arched petiole and short ovipositor; it is similar to parvulus from which it is distinguished by its smooth vertex.

### Spathius sequoiae Ashmead (Figs 17 A-E)

Spathius sequoiae Ashmead (1888)1889:625; Matthews 1970:44.

Spathius canadensis Ashmead 1891:2; Matthews 1970:47. New synonymy.

Spathius clavipennis [sic] Ashmead 1892:257. Nomen nudum.

Spathius californicus Ashmead 1893:70. Synonymized by Matthews 1970:44.

Spathius tomici Ashmead 1893:71. Synonymized with canadensis by Matthews 1970:48. New synonymy.

Spathius claripennis Ashmead 1893:72. Synonymized with *canadensis* by Matthews 1970:47. **New synonymy**.

Spathius brunneri Viereck 1912:627. Synonymized by Matthews 1970:44.

Female.—Color: body honey yellow to light brown, base of gaster and apex of petiole usually darker; legs often lighter than body; antenna yellow basally becoming brown at apex; wings nearly hyaline, often with indistinct weak bands. Body size: 2.5-4.0 mm. Head: face transversely striaterugulose; frons transversely strigate, sometimes nearly smooth; vertex weakly transversely strigate medially, often nearly smooth; temple smooth or weakly acinose; malar space about 1/2 eye height; vertex narrow, ocellar-ocular distance about equal to ocellar-occipital distance; antenna with 22-32 flagellomeres. Mesosoma: propleuron rugulose; pronotum rugulose, pronotal

groove weakly indicated, weakly scrobiculate; mesoscutal lobes acinose, notauli scrobiculate and meeting at scutellum in narrow triangular rugose area, often with two distinct longitudinal carinae; scutellum acinose; mesopleural disc transversely striate, often acinose or smooth directly above precoxal sulcus, subalar area transversely costate; precoxal sulcus slightly more than half length of mesopleuron, weakly scrobiculate; propodeum rugose, areola distinct and often long and narrow, basal carina often short. Wings: fore wing vein 2RS equal to or slightly longer than vein 3RSa, vein 3CU not on same line as vein 1CU, thus short segment of vein 2CU present, vein 1cu-a beyond vein 1M; hind wing vein r-m slightly less than 1/2 length of vein 1M. Legs: fore tibia with single or irregular double and occasionally triple row of 10-30 spines along anterior edge; hind tibia with 2-5 spines at outer apical lobe. Metasoma: petiole strongly arched at base in lateral view, rugose dorsally on basal half, costate on apical half; second metasomal tergum acinose or weakly strigate on basal 2/3, occasionally nearly smooth, remainder of terga smooth; ovipositor equal to or slightly longer than metasoma.

Male.—Essentially as in female.

Distribution.—Widespread in Northern North America, from Maine to higher elevations in North Carolina, west to Alaska and California.

Biology.—This species attacks a wide variety of scolytids in coniferous trees. Matthews considered most host records from elm for canadensis, as he defined the species, to belong to his new species benefactor, which is considered a synonym of laflammei in the present study (Matthews 1970). Recorded hosts are as follows: Alniphagus aspericollis Lec., Cryphalus pubescens Hopk.., Dendroctonus obesus (Mann.), D. pseudotsugae Hopk., Dryocoetes autographus (Ratz.), Ips pini (Say), Lechriops californicus (Lec.), Orthotomicus caelatus (Eichh.), Pityophthorus balsameus Blkm., Phloeosinus

punctatus Lec., P. sequoiae Hopk., Pissodes sp., Polygraphus rufipennis (Kirby), Pseudohylesinus nebulosus (Lec.), P. sericeus (Mann.), Scolytus laricis Blkm., S. piceae (Swaine), S. tsugae Swaine. S. unispinosus Lec., S. ventralis Lec. (Coleoptera: Scolytidae).

Comments.—Matthews (1970) retained sequoiae and canadensis as separate species but considered the separation as tentative. We have seen all the specimens that Matthews studied and several more series and consider the species to be one fairly variable species. This species is similar to rubidus but can be separated by the ovipositor which is equal to or longer than the metasoma (in rubidus it is shorter than the metasoma and usually not longer than the gaster).

### Spathius stigmatus Matthews (Figs 18 A–H)

Spathius stigmatus Matthews 1970:32.

Female.—Color: head, mesosoma, and petiole light brown, metasoma beyond petiole dark brown; legs light brown, hind tibia white on basal 1/4; antenna honey yellow, apical 6-8 flagellomeres light brown to brown; fore wing mostly darkly infumated except for subhyaline band at apex and across middle from base of stigma, stigma yellow on basal 1/3. Body length: 3.5-5.0 mm. Head: eyes small, malar space 3/4–4/5 eye height; face transversely striate; frons transversely striate; vertex finely striate, smooth around ocelli; temple finely striate; vertex broad, ocellar-occipital distance about 1.5 times ocellar-ocular distance; temple broader than eye width; antenna with 16-19 flagellomeres, those beyond third less than twice as long as wide, all flagellomeres with a circle of 4 long erect setae on apical rim. Mesosoma: propleuron, including flange, smooth; pronotum longitudinally carinate, pronotal groove scrobiculate anteriorly and over pronotal collar, absent posteriorly; mesoscutal lobes acinose; notauli scrobiculate, meeting at scutellar furrow in triangular

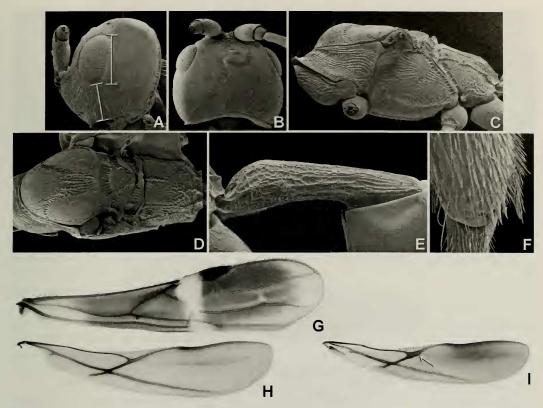


Figure 18. Spathius stigmatus Matthews, female. A, head lateral view with eye height and malar space measurement indicated; B, head dorsal view; C, mesosoma lateral view; D, mesosoma dorsal view; E, petiole lateral view; F, outer apical margin of hind tibia; G, fore wing; H, hind wing. Male, I. hind wing with stigma-like swelling indicated.

carinate-rugulose area; scutellum acinose, scutellar furrow with 7-8 evenly spaced cross carinae; mesopleural disc longitudinally carinate, subalar area rugose; precoxal sulcus shallow, distinctly scrobiculate; propodeum acinose dorsally, becoming rugose apically, acinose laterally, carinae and areola obscured, lateral carinae distinct. Wings: fore wing vein 2RS shorter than vein 3RSa, vein 3CU on same line as vein 1CU; hind wing vein r-m about 1/2 length of vein 1M. Legs: fore tibia with single row of stout spines along anterior edge; hind tibia with 4 stout spines at outer apical rim; hind coxa angled at base but antero-ventral tooth not distinct. Metasoma: petiole distinctly arched at base in side view, dorsally rugose at base, acinose medially, striate apically; second tergum finely striate on basal 1/3-1/2, remainder of terga smooth; ovipositor nearly twice as long as body.

*Male.*—Essentially as in female; hind wing with stigma-like swelling at junction of veins SC+R, r-m, R, and RS.

*Distribution.*—Occurs over entire eastern North America, Quebec to Florida, west to Ontario, Wisconsin and Texas.

*Biology.*—The only reliable rearing record is from *Magdalis olyra* in hickory. It has also been associated with other cerambycids and clerids in hickory.

Comments.—This species is distinct with its small eyes and long malar space and very long ovipositor.

#### Spathius trifasciatus Riley (Figs 19 A–G)

Spathius trifasciatus Riley 1873:106; Matthews 1970:66.

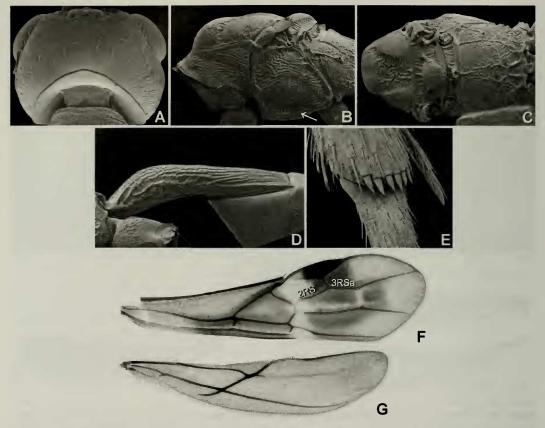


Figure 19. Spathius trifasciatus Riley, female. A, head dorsal view; B, mesosoma lateral view with carina along lower margin of sternalus indicated; C, mesosoma dorsal view; D, petiole lateral view; E, outer apical margin of hind tibia; F, fore wing with 2RS and 3RSa indicated; G, hind wing.

Spathius unifasciatus Ashmead 1893:70, 72. Synonymized by Muesebeck and Walkley 1951:170.

Female.—Color: body usually dark brown; head often honey yellow, scape, pedicel and basal third of flagellum honey yellow, remainder of flagellum brown; mesosoma occasionally light brown or honey yellow, mesoscutal lobes and propodeum always darker; petiole and metasomal terga 2-3 often honey yellow; legs often brown or honey yellow, tibiae with lighter band on basal 1/5; fore wings distinctly banded, basal 1/3 of stigma yellow, tegula usually yellow. Body length: 3.0-6.5 mm. Head: face transversely rugulose-striate; frons rugose, rugae usually transverse but occasionally longitudinal; vertex striate anteriorly diminishing to

smooth at occipital carina; temple finely striate, occasionally near eye and to malar space; vertex broad, ocellar-occipital distance about twice ocellar-ocular distance; temple nearly as wide as eye, in dorsal view bulging slightly beyond eye margin; malar space slightly less than 1/2 eye height; antenna with 25-37 flagellomeres. Mesosoma: propleuron transversely rugose, propleural flange smooth; pronotum carinate or porcate posteriorly, often rugose anteriorly, pronotal groove scrobiculate over pronotal collar; mesoscutal lobes strongly acinose, notauli strongly scrobiculate, meeting at scutellar furrow in deep triangular rugose area; scutellum acinose, scutellar furrow usually with 5 cross carinae; mesopleural disc longitudinally costate, the costae stronger dorsally, sub-

alar groove rugose; precoxal sulcus bordered below by distinct carina usually extending from epicnemial carina to mid coxa, several longitudinal carinae extending from middle of precoxal sulcus to mid coxa; propodeum rugose laterally, dorsal areas acinose, carinae not always distinct, areola transversely rugose or costate. Wings: fore wing vein 2RS longer than vein 3RSa, vein 3CU not interstitial with vein 1CU, thus small section of vein 2CU present; hind wing vein r-m about 1/3 length of vein 1M. Legs: fore tibia with several irregular rows of spines along anterior edge; hind tibia with 6-10 spines at outer apical rim; antero-ventral tooth at base of hind coxa sharply pointed. Metasoma: petiole distinctly arched in side view at base, rugose dorsally on basal half, costate on apical half; second tergum delicately striate or acinose at base; remainder of terga smooth and polished, occasionally with weak punctate band across terga anterior to setal band; ovipositor slightly longer than metasoma.

Male.—Essentially as in female except femora are more swollen and the fore tibia has fewer spines along the anterior edge.

Distribution.—Eastern U. S. from New York south to North Carolina, west to Wisconsin, Kansas and Texas.

Biology.—The only reliable records are rearings from *Scolytus quadrispinosus* Say (Coleoptera: Scolytidae) in hickory.

Comments.—The precoxal sulcus, which is bordered below by a distinct carina, is characteristic for this species and brunneus from which it can be separated by the longer ovipositor (longer than the metasoma in trifasciatus, shorter than the metasoma in brunneus), flat scutellum (swollen in brunneus), deeper area on mesoscutum where notauli meet, and darker color (mostly light brown to dark orange in brunneus).

### COMMENTS ON THE BIOCONTROL OF THE EMERALD ASH BORER

Although species of *Spathius* have been reared from a variety of bark beetle

families, only a few are associated with *Agrilus* and other Buprestidae. Notes on these species are presented below.

Spathius agrili Yang (Figs 20A–H). This species was recently described from China (Yang et al. 2005) where it was reared from the emerald ash borer. Although only preliminary biological studies have been performed, it appears that this species is specific to the emerald ash borer and represents a very promising candidate for introduction into North America. Spathius agrili is similar to S. leiopleuron but differs in having the petiole in dorsal view narrower and the propodeum more closely sculptured than in leiopleuron.

Spathius brunneus Ashmead. This species has been recorded from Agrilus fallax as well as Scolytus muticus and is apparently not specific to buprestids.

Spathius floridanus Ashmead. This species has been reared from the buprestids Agrilus anxius and A. bilineatus (under the name Spathius simillimus) and Chrysobothris femorata and from several cerambycids and curculionids. More importantly, it has been reared from galleries of the EAB in Michigan. Thus, it represents the most promising North American species that could be utilized in a biocontrol program.

Spathius species. Among specimens reared in association with the emerald ash borer in Michigan were one female and three males of an apparently new species that does not accurately fit into the key presented above. The female will run to *impus* but has a longer ovipositor. Until further females of this species are obtained, we have decided not to describe it at this time. If it proves to be a distinct species, it will add one more possibility for the control of the emerald ash borer.

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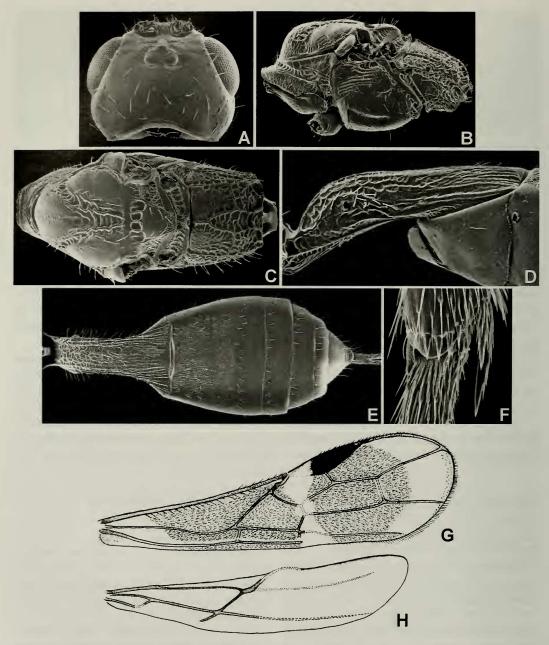


Figure 20. Spathius agrili Yang, female. A, dorsal view of head. B, mesosoma lateral view; C, mesosoma dorsal view; D, petiole lateral view; E, petiole and metasoma dorsal view; F, outer apical margin of hind tibia; G, fore wing; H, hind wing. (Yang et al. 2005, used with permission.)

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#### LITERATURE CITED

- Ashmead, W. H. 1888(1889). Descriptions of new Braconidae in the collection of the U. S. National Museum. *Proceedings of the U. S. National Museum* 11: 611–671.
- ——. 1891. Descriptions of some new Canadian Braconidae. Canadian Entomologist 23: 1–7.
- ——. 1892. *In*: Hopkins, Some bred West Virginia Braconidae. *Insect Life* 4: 256–259.
- . 1893. Descriptions of new braconids bred by Prof. A. D. Hopkins. *Canadian Entomologist* 25: 67–79.
- Bauer, L. S., H-P. Liu, R. A. Haack, R-T. Gao, T-H. Zhao, D. L. Miller, and T. R. Petrice. 2005. Update on emerald ash borer natural enemies in Michigan and China. Pp. 71–72 in: V. Mastro and R. Reardon, eds. Proceedings of the Emerald Ash Borer Research and Technology Meeting, Romulus, MI. USDA FS FHTET-2004-15.
- Belokobyl'skij, S. 1992. On the classification and phylogeny of the braconid wasp subfamilies Doryctinae and Exothecinae (Hymenoptera, Braconidae) (in Russian). Part I. On the classification. Entomologicheskoe Obozrenie 71: 900–928. [English translation: 1993, Entomological Review 72: 109–137.]
- ——1998. Subfamily Doryctinae. Pp. 50–109 in: P. A. Ler, ed. Key to the insects of the Russian Far East. Vol. 4, Neuropteroidea, Mecoptera, Hymenoptera, Part 3, Ichneumonoidea, Braconidae. Vladivostok. 708 pp.
- Cameron, P. 1905. On the phytophagous and parasitic Hymenoptera collected by Mr. E. Ernst Green in Ceylon. *Spolia Zeylanica* 3: 67–97.
- Foerster, A. 1862. Synopsis der Familien und Gattungen der Braconiden. Verhandlingen des Naturhistorischen Vereines der Pruessischen Rheinlande und Westphalens 19: 226–228.
- Haack, R. A., E. J. H. Liu, K. R. Marchant, T. R. Petrice, T. M. Poland, and H. Ye. 2002. The emerald ash borer: a new exotic pest in North America. Newsletter of the Michigan Entomological Society 47: 1–5.
- Harris, R. A. 1979. A glossary of surface sculpturing. Occasional Papers of Entomology, California Department of Food and Agriculture, no. 28, 31 pp.
- Herms, D. A., D. G. McCullough, and D. R. Smitley. 2004. Under Attack. *The American Nurseryman*, October 2004. pp. 20–26.
- Marsh, P. M. 1997. Subfamily Doryctinae. Pp. 206–233 in: R. A. Wharton, et al., eds. Manual of the New World genera of the family Braconidae (Hymenoptera). Special Publication of the International Society of Hymenopterists No. 1. 439 pp.
- 2002. The Doryctinae of Costa Rica (excluding the genus Heterospilus). Memoirs of the American Entomological Institute 70: 1–319.

- Matthews, R. W. 1970. A revision of the genus *Spathius* in America north of Mexico (Hymenoptera, Braconidae). *Contributions of the American Entomological Institute* 4 (5): 1–86.
- —— and P. M. Marsh. 1973. Notiospathius, a new Neotropical genus (Hymenoptera: Braconidae). Journal of the Washington Academy of Sciences 63: 73–75.
- Muesebeck, C. F. W., L. M. Walkley. 1951. Family Braconidae. Pp. 90–184 in: C. F. W. Muesebeck et al., eds. *Hymenoptera of America North of Mexico. Synoptic Catalog.* USDA Agricultural Monograph No. 2. 1420 pp.
- Nees von Esenbeck, C. G. 1818. Appendix ad J. L. C. Gravenhorst conspectum generum et familiarum Ichneumonidum, genera et familiam Ichneumonidum adscitorum exhibens. Nova Acta Academiae Caesoreae Lepoldino-Carolinae 9: 299–310.
- ——. 1834. Hymenopterorum Ichnemonibus Affinium Monographiae 1: 1–320. Stuttgart, Tubingen, Cotta.
- Nixon, G. E. J. 1943. A revision of the Spathiinae of the Old World (Hymenoptera, Braconidae). *Transactions of the Royal Entomological Society of London* 93: 173–456.
- Provancher, L. 1880. Faune Canadienne: les Insectes Hymenopteres. *Naturaliste Canadienne* 12: 161–180.
- ——. 1886. Additions a la Faune Canadienne -Hymenopterologique. *Naturaliste Canadienne* 16: 121–180.
- Riley, C. V. 1890. *In*: Riley and Howard, Some of the bred parasitic Hymenoptera in the National Collection. *Insect Life* 2: 348–353.
- . 1873. Fifth Annual Report on the Noxious, Beneficial and Other Insects of the State of Missouri. Regan & Carter, Jefferson City, MO. 160 pp.
- Rossi, P. 1794. Mantisa Insectorum Vol. 2: 1–154. Pisa, Polloni.
- Smith, F. 1859. Catalogue of hymenopterous insects collected by Mr. A. R. Wallace at the islands of Aru and Key. *Journal of the Linnaean Society* 3: 132–178.
- Szépligeti, G. V. 1904. Sudamerikanische Braconiden. Annales Musei Nationalis Hungarici 2: 173–197.
- ——. 1902. Tropische Cenocoeliden und Braconiden aus der Sammlung des Ungarischen National-Museum II. Termeszetrajzi Füzetek 25: 39–84.
- Viereck, H. L. 1912. Contributions to our knowledge of bees and ichneumon-flies, including descriptions of twenty-one new genera and fifty-seven new species of ichneumon-flies. *Proceedings of the U. S. National Museum* 42: 613–648.
- Walker, F. 1874. Descriptions of some Japanese Hymenoptera. *Cistula Entomologica* 1: 301–310.
- Wharton, R. A. 2006. The species of *Sternaulopius* Fischer (Hymenoptera: Braconidae, Opiinae) and the Braconid sternaulus. *Journal of Hymenoptera Research* 15: 317–347.

- Wharton, R. A., P. M. Marsh, and M. J. Sharkey, eds. 1997. *Manual of the New World genera of the family Braconidae (Hymenoptera)*. Special Publication of the International Society of Hymenopterists No. 1, 439 pp.
- Wilkinson, D. S. 1931. On the Indo-Australian and Ethiopian species of the braconid genus Spathius (Hymenoptera). Transactions of the Royal Entomological Society of London 79: 505–530.
- Yang, Zhong-Qi., J. S. Strazanac, P. M. Marsh, C. van Achterberg, and Won-Young Choi. 2005. First recorded parasitoid from China of *Agrilus plani*pennis: a new species of *Spathius* (Hymenoptera:

- Braconidae: Doryctinae). Annals of the Entomological Society of America 98: 636-642.
- Zaldivar-Riverón, A., S. A. Belokobylskij, V. León-Regagnon, J. J. Martínez, R. Briceño, and D. L. J. Quicke. 2007. A single origin of gall association in a group of parasitic wasps with disparate morphologies. Molecular Phylogenetics and Evolution 44: 981–992.
- , S. A. Belokobylskij, V. León-Regagnon, J. J. Martínez, R. Briceño, and D. L. J. Quicke. 2008. Molecular phylogeny and historical biogeography of the cosmopolitan parasitic wasp subfamily Doryctinae (Hymenoptera: Braconidae). *Invertebrate Systematics* 22: 345–363.